Is habitat restoration effective?

Much of what the Wild Trout Trust (WTT) undertakes on a routine basis can be described as identifying, and finding solutions for, habitat bottlenecks that constrain wild fish populations. In terms of wild trout, the existence of a bottleneck is defined as a shortage of (or a lack of access to) habitat features that are crucial to each stage of a trout's lifecycle. This approach is particularly attractive because it focuses the practitioner on finding and fixing the actual problems facing a watercourse. It is also based on a fundamental principle of ecology; the idea of an ecological niche. By its simplest definition:

A niche is the set of conditions and resources needed by an individual (or species) in order to practice [sic] its way of life (after Hutchinson [1]).

Habitats that do not provide this full set of conditions and resources pose a serious problem for species' survival within that system. Furthermore, it is suggested that bringing conditions back within niche limits should produce more consistently positive results than altering aspects that already fall within niche limits [2]. This poses interesting problems when we assess efficacy of habitat restoration - for instance:

- How to discern whether the problem has been correctly identified (i.e. that the "outside niche boundaries" condition is applicable)
- How to have confidence that restoration brings conditions back within niche boundaries

Part of the challenge includes the known difficulties of accounting for the high levels of natural variation present within ecosystems. As a prime example, the choice of survey methods and how diligently a method is applied has been shown to be capable of totally reversing the interpretation of whether restoration has been effective[3]. Consequently, it is highly pertinent to pose the question:

"**How confident can we be that the approaches to habitat enhancement that we routinely recommend are likely to be beneficial?**"

Consideration of published information relating to three key life cycle stages of trout (spawning, juvenile and adult) enables the description of current understanding of what wild trout require in order to thrive. Subsequent examination of studies measuring the success of efforts to provide for these requirements enables us to address the question of how effective habitat restoration is likely to be.

Spawning habitat

A variety of studies that characterise spawning sites (e.g. [4-12] summarised in [13]) have been used to derive generalised tolerance ranges for factors such as particle size, flow velocity and depth for brown trout breeding success. Furthermore, an extensive review article[14] that considers each of the above factors, as well as incorporating conditions inside the gravel beds, suggests the following for brown trout spawning habitat requirements:

Gravel/pebble particles between 16 and 64mm are favoured with depths and flow velocities of 15–45 cm and 20–55 cm per second respectively. Developing eggs can stand quite low oxygen levels (down to 0.8mg/l) but hatching eggs require at least 7 mg/l (at 5.5°C). The inter-relationship between temperature and oxygen demand/solubility in water is indicated by a greater minimum requirement for oxygen at higher temperature (e.g. 10mg/l at 17°C compared to 7mg/l at 5.5°C). Contact between developing eggs and oxygen-rich water can be dramatically reduced by prevalence of fine sediment (<2mm in diameter) that can block the spaces between the gravel particles. In addition, very fine silt and clay (<0.125mm) particles are capable of blocking the pores involved in gas-exchange on the outer membrane of the eggs themselves.

Therefore, as well as the existence of sufficiently cool water, a requirement for gravel "sorting" is implied - where pebbles of preferred diameters occur together and fine sediment is washed away. Gravel sorting, with the attendant redistribution of fine silt, may be observed following installations of large woody debris (e.g. Fig. 1) – that could indicate the potential value of deliberate introductions of such material.

Figure 1: Trout redd next to flow deflector installed on the river Wandle

It is important to appreciate additional factors that <u>may not be related to the inherent proportion of eggs that successfully hatch</u> can also influence selection of spawning site or spawning success. For example, predation on Atlantic salmon eggs by bullheads varies according to gravel particle sizes – with lower than 5% egg predation in substrate <37mm versus up to 88% predation in substrates of 67mm diameter[15]. This is completely opposite to the general trend of larger substrate sizes (and the attendant improved circulation of intra-gravel water) related to successful salmon fry emergence[15]. More subtle still is the occurrence of "co-selection" of habitat attributes according to simultaneous – but totally separate - sets of needs. For example, many trout prefer to migrate upstream towards smaller headwater riffle habitats in order to spawn. However, for some larger trout, the requirement to secure high quality overwintering lies can lead to a conflict between ideal habitat for developing eggs/fry and the habitat suitable for their own overwinter survival. In these cases, the proximity of large woody debris cover/deep pool habitat to gravel of suitable size for egg development could lead to larger fish spawning successfully in main river reaches downstream of the normal "preferred" upstream reaches[13]. This interplay between optimal egg/fry development conditions and the needs of the breeding adult population means that spawning habitat restoration should not solely focus on gravel size and flow characteristics. Provision of both adult cover as well as silt-free, size-sorted gravel substrates will be important components of effective solutions to spawning habitat bottlenecks.

Figure 2: Brash installation (left) and riparian vegetation re-establishment through grazing exclusion (right) creating ideal habitat for juvenile trout

Assessment of spawning habitat restoration efficacy

There is good evidence to suggest that trout populations limited by a lack of access to good quality spawning substrate can be successfully increased following deliberate creation of spawning habitat in degraded river reaches. A study in Sweden assessed the density of juvenile trout less than one year old ("0+" trout) in the period between 1992 and 2003[16]. The density of juveniles became significantly greater in reaches that had both boulders and spawning gravels introduced when compared to reaches in which only boulders were installed. Furthermore, the measured egg to fry survival rate was significantly greater in the gravel and boulder treatment than in the boulder-only treatment. The authors suggest that this was due to increased proportions of fine particulate material in substrate at the boulder-only treatment. The increase in juvenile density was positively correlated to the area of spawning beds created (m^2 of introduced gravel per 100 m^2 of stream). These findings indicate that, in this case, the density of juvenile brown trout was limited by the availability and quality of spawning substrate rather than by structural complexity of the habitat. The success of artificially importing spawning gravels, in concert with improving structural complexity, in increasing juvenile trout densities was clearly demonstrated.

Juvenile habitat

The life-cycle stage that comes as trout (and other salmonid fish) first emerge from the gravels and make the switch to defending a small territory and foraging for food is recognised as potentially critical in determining how well a population will fare (e.g. [17, 18]). The importance of shelter that increases the proportion of juvenile salmonids that successfully overwinter has been highlighted for brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and masou or "cherry" salmon (*Oncorhynchus masou*) amongst other species (e.g.[2, 17-19]). It is a characteristic of salmonid fish that the majority of whole lifecycle mortality occurs in juvenile stages and the transition from maternal provisioning (i.e. absorption of the yolk sac) to self feeding and territory acquisition[20].

In terms of the factors that could drive this pattern of mortality in salmonid fish, there is evidence that combined influences of shelter (limiting both predation and reducing the rate of energy expenditure) and food acquisition could be operating. For example, studies of juvenile cutthroat trout (*Oncorhynchus clarki*) indicate that whilst overall growth-rate was determined by food supply – the amount of mortality due to predation was controlled by availability of cover. In fact, the addition of cover reduced the amount of predation by 50% in the cutthroat trout streams that were studied[21]. Surprisingly though, overwinter survival of juvenile (1+) cutthroat trout was found to be unaffected by body mass – i.e. rapid early growth did not necessarily increase the chances of survival [21]. However, this measurement would not, of course, include those 0+ fish that had already starved or succumbed to disease or predation prior to entering their first overwinter period.

In Atlantic salmon studied in Vermont, USA, mortality due to starvation that was determined by the availability of foraging habitat has been demonstrated by using a combined "bioenergetic" and habitat-availability approach[20]. The measurement of stable Cesium (C^{133}) that is taken up naturally from the food-web in juvenile fish tissues is an elegant way of deriving the rate at which prey have been consumed. By stocking out groups of salmon fry and then re-sampling them at several future time-points their actual (measured) consumption rate as well as their spatial location within the habitat could be compared to model predictions. The predictions of feeding rate based on habitat selection made by the model improved later in the study – possibly a reflection of the time taken for fry to "learn" how and where to forage effectively during the early stages of the trial[20]. In addition, the natural conditions present soon after fry emerge (and when the experimental fish were stocked) provided only very limited amounts of natural food. Many young fish starved during this period – and it was this mortality that was the most important in terms of determining population structure[20]. The streams studied did not appear to vary in the degree of predation that they suffered and the availability of food was thought to be more important than energy expenditure due to competition between salmon fry[20].

Other studies provide evidence that juvenile refuge habitat is important for limiting the rate of energy expenditure. The presence of shelter significantly reduces the metabolic costs required to maintain juvenile salmon body condition [22] – and could consequently make net energy gains even when food availability is equal in different habitats. This effect was noted even though transparent shelter "ledges" were used to remove any confounding influence of light levels or visual stimuli – such as changing territorial behaviour in response to reduced visibility of rivals. Fish were observed to shelter around the edges, rather than beneath, the perspex ledges and their rate of oxygen uptake was 30% lower than in the absence of shelter[22]. As a further example of variation in energy expenditure, aggressive competition (both within and between Atlantic salmon and brown trout) for overwintering refuges in juvenile fish is observed to be highly intense when refuges are in short supply[23]. Existing residents are less likely to leave a refuge than an intruder when disputes arise and competitive interactions are reduced when refuges are plentiful [23]. The intense struggle to oust a competitor when refuges are in short supply is likely to make especially severe demands on the energy reserves of juvenile fish who are not the first to locate a particular refuge.

The importance of constraints imposed by a lack of juvenile habitat and the associated costs to the majority of individuals is further implied by observed relationships between habitat complexity and juvenile “fitness” (survival and reproduction). Increased physical complexity in habitat is associated with a reduced gap in fitness between dominant juvenile individuals relative to subordinates[24]. The size of individual territories were reduced – as was the degree of resource monopolisation by dominant individuals [24]. In other words, a greater number of juveniles could co-exist and thrive in more complex habitats.

The combined findings above suggest that the previously-noted effect of cover habitat causing reduced predation is mirrored by similar effects of reduced energy expenditure and reduced intra-specific competition. The great importance of food availability and foraging habitat is also highlighted. Consequently, the effects of creating juvenile cover habitat will stem from a combination of the actions of these factors – as well as the ever-present need to correctly identify the problems facing a particular system.

Assessment of juvenile habitat restoration efficacy

In terms of restoration, adding complexity to channelized streams can reduce early winter weight loss in juvenile fish due to increased availability of refugia. In other words, the presence of refugia reduces the rate at which weight is lost – even though fish in both restored and un-restored reaches are losing weight (i.e. starving) during early winter period[25]. Although fish in un-restored channels catch up by growing faster later in winter, the cost of this may have long term fitness impacts[25]. For example, a range of impacts on salmonid fish have been recorded after early starvation followed by a period of compensatory faster growth. Impacts include impaired locomotor performance in Coho salmon (*Oncorhynchus kisutch*), muscle lesions in arctic char (*Salvelinus alpinus*), fat deposition rate, growth rate and age at sexual maturation in Atlantic salmon (*Salmo salar*) that were noted in a meta-analysis of studies that spanned a wide range of fish, birds, mammals, insect and amphibian examples[26].

A very clear and direct relationship between habitat works designed to increase the availability of juvenile habitat and subsequent increases in population parameters for three salmonid species was noted during an 8-year study of two Oregon streams. One stream was restored and one was allowed to remain in its original condition. In comparison to the un-restored stream, increasing juvenile overwintering habitat significantly increased number of smolts produced by migratory species (steelhead trout *Oncorhynchus mykiss*, Coho salmon *Oncorhunchus kisutch* and Coastal cutthroat trout *Oncorhynchus clarki* as well as increasing the downstream migration output of juveniles from “stream-resident" trout species (*Oncorhynchus spp*.) [27] . The summer population density of adult "resident" trout did not increase – as the adult habitat was thought to be already at the maximum carrying capacity for adult fish[27].

With reference to the previously identified importance of available food, significant benefits to stream invertebrate diversity (as well as a significant summer cooling effect) have been measured within marginal brash installed as juvenile trout habitat[28]. As a consequence, it is possible that the major juvenile-mortality-controlling factors of reduced predation, reduced energy expenditure and increased opportunities for feeding could be conferred by introducing submerged brash cover. Clearly, there is a limit to the extent to which these benefits will translate to population-level effects. Modelling suggests that the ceiling above which increasing early juvenile survival will not confer any additional adult population gains should be around 20% survival[17]. Typically early juvenile survival is much lower than this. For example, Elliott's work in a Cumbrian stream indicates survival of between approximately 5% and 9% within only the first 60 days following emergence for 8 separate year classes of brown trout (see Fig. 3 of [29]).

Of course, creation of juvenile habitat cannot be a universal panacea. In addition to the previously stressed notions that there is little point in manipulating habitat that is already present in excess[2], it is important to understand that within-channel manipulations will be unable to over-ride impacts that are not simply related to physical habitat structure. A perfect example of this is the lack of measurable effects of restoring juvenile fish habitat in several channelized boreal streams of Finland[30]. The authors concluded that, in addition to a lack of success in creating some desired physical features within the channel, no "within-channel" manipulation would be able to over-ride the significant negative impacts of large-scale deforestation. As a result, any in-channel creation of juvenile (or indeed any other life-stage) habitat must be accompanied by an understanding of the major limitations and impacts operating both at local and catchment scales.

Adult Habitat

There are long-established mathematical relationships between "cover" habitat (including overhead and submerged cover as well as boulder and rubble cover, stream flow and stream depth) and the standing crop (mass per unit area) of brown trout. These include both total standing crop (e.g.[31]) as well as the standing crop of different life-stages – including adult trout (e.g.[10]). On the one hand, such relationships are unlikely to remain quantitatively predictive across a wide range of systems, e.g. due to the presence of local genetic adaptation[2]. Conversely, it is still generally valid to conclude that cover habitat, and the formation of pool habitat, particularly due to the presence of riparian vegetation that provides sufficient resistance to bank erosion, is vital for stream-resident adult brown trout (after e.g. [10, 31]). In addition to established empirical relationships between natural habitat structure and brown trout populations, there are many individual studies that report increases in adult brown trout biomass following deliberate introduction of such features (e.g.[32]). Irish rivers with a low natural supply and retention of Large Woody Debris had "partial span" large wooden structures installed. Following these installations, there was an increase in variety of flow-depth and pace as well as fine sediment distribution. Along with physical habitat changes, an increased trout density and biomass in restored reaches was observed 1 and 2 years after works (relative to un-restored reaches). The physical “condition” (length to mass ratio) of individual fish did not differ between treatment and control[32]. However, such post-restoration population improvements are far from universally observed. The following report section appraises the current state of knowledge with respect to the relationship between structural habitat alterations and subsequent biological responses.

Figure 3: Importing cover structure that adult trout can use

Adult habitat/significant structural complexity restoration efficacy

At the heart of using habitat alteration as a means of biodiversity conservation is an implied assumption that:

“*Changes in physical habitat structure can result in a response by the biological component of the system under consideration*”

However, it is unlikely that such a simple relationship can always – or even usually – be observed in practice. This has been exemplified via investigations of reaches on tributaries of the River Ume system in Sweden that compared:

- degraded sites that have been restored
- degraded sites that remained un-restored
- reference “un-degraded” sites

The investigations found no evidence that physical restoration of degraded sites resulted in increased diversity in either fish or invertebrate species[33]. The authors concluded that any biological response to physical structural alteration will be critically dependent on successfully manipulating habitat at the specific spatial scale that is relevant to particular target organisms[33]. With specific regard to trout populations, this will require reference to the ranges of defined characteristics (such as pool depth, flow velocities and substrate diameters) for each of the three key life-stages; adult, juvenile and spawning.

The relatively greater availability of quantitative data sets for macroinvertebrate studies is likely to be illustrative in addressing the questions of fundamental relationships between structural alterations and biotic response. An extensive review [34] recently found only 2 projects undertaken by 18 separate project author groups actually reported increased macroinvertebrate taxa richness (number of types of invertebrate) in response to deliberate increases physical habitat complexity. The authors further stress that far more fundamental impacts were usually likely to constrain invertebrate taxa richness (i.e. water quality, flow regime) than simple physical characteristics[34]. Despite this, most restoration projects focus on physical structural interventions[34]. However, this same review study also gives supporting evidence that – where water quality and riparian habitat quality is healthy – increased in-channel habitat complexity can be related to increased invertebrate diversity. The review found that out of the 12 studies performed in rivers with good riparian buffer strips - five showed a statistically significant increase in invertebrate taxonomic richness following increases in physical habitat complexity[34]. The authors did not stress that another fundamental constraint on increases in taxon richness also depends on their being available sources of colonisation. This, along with statistical and sampling sensitivity, may account for some of the remaining 7 studies that did not show increased invertebrate diversity.

With specific regard to salmonid fish, a very well-designed systematic meta analysis was undertaken to examine the outcomes of large woody debris (LWD) introduction projects aimed at improving salmonid populations[35]. The methods that these authors employed were those that are used to assess efficacy of medical interventions and are specifically designed to avoid both conscious and unconscious biases. The overall conclusion of this objective study was that the widespread use of LWD additions to channels are not supported by the scientific evidence base that they examined [35]. Whilst there was an overall small but statistically significant positive benefit (on average) to population densities following LWD introduction – there was evidence that the available information had a proportional over-representation of positive outcomes[35]. The very elegant (and simple) technique called an “Egger Test Funnel plot” can be used to indicate whether the overall available information is balanced – or conversely – shows bias towards either negative or positive outcomes. The funnel plot produced during the review of LWD introduction studies indicated that there was a relative lack of small studies reporting negative effects[35].

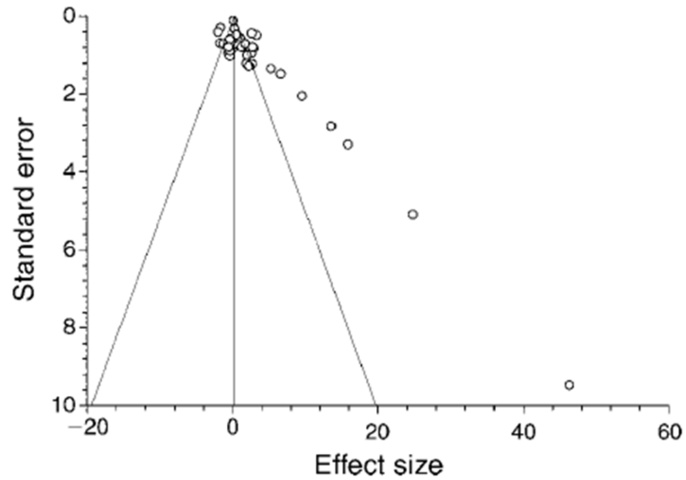

Figure 4: Eggers Funnel plot reproduced from[35] that shows the relative lack of smaller (studies lower down the vertical axis) reporting less positive results that should appear to the left hand side of the graph.

This extremely rigorous study is worthy of serious attention – and very much worth extending upon. At the time of their review (2009) the authors regretted the unavoidable information loss from the starting pool of 179 studies that had to be reduced to only 17. This small remaining pool contained the only examples where viable inter-study comparisons could be made using the specific methodology adopted. This frustrating difficulty, along with additional pragmatic limitations facing many conservation practitioners, is noted:

"*There are many other factors that are not as easy for practitioners to measure with limited budgets, time, and resources. These include water quality (diffuse pollution, acid episodes, or dissolved oxygen content), flow rates, and pathogen abundance, all of which are known to affect fish populations. The carrying capacity of a waterway may be limited by a factor that is not modified by the installation of an in-stream structure, and these factors need to be addressed to allow any potential benefits of in-stream structures to be realized. The age of the in-stream structure may also have an impact, as older structures may decay and therefore become less (or more) effective. Engineered in-stream structures do increase salmonid abundance in some instances. Proponents of in-stream restoration suggest that in-stream structures should work in otherwise healthy waterways (O'Grady 2006) and suggest that poor water quality may be a confounding factor (P. Roni, I. Cowx, and M. O'Grady, personal communication). Further empirical evidence is required to corroborate this hypothesis, which is not testable with the available data. Practitioners therefore need to consider the state of the waterway as well as its width prior to rehabilitation work being carried out, as water quality or amount of existing modification may impact greatly on effectiveness of rehabilitation schemes*"[35].

The concluding sentence from the above quote is yet another reinforcement of the principle that the primary problems – and appropriate solutions – must be identified if physical habitat manipulation is to be relevant and effective. A salutary example of the potential of other impacts to over-ride any in-channel modifications is found in the attempted restoration of upper reaches of the Oulujoki water course in north-eastern Finland. Here, rehabilitation of channelized streams clearly increased streambed complexity, but did not have detectable effects on brown trout stocks in either of the rehabilitation schemes (addition of LWD or large stones), except for age-2+ and older fish which decreased in abundance compared to control reaches[36]. A severe drought after rehabilitation in late summer 2002 reduced densities of trout to a low level in all streams, overriding any local effects of rehabilitation[36]. Similarly, recalling the earlier assertion that physical modifications must impact the relevant spatial scale for particular target organisms, it has been noted that trees larger than 60cm in diameter were by far the most effective at actually increasing pool frequency in British Columbian streams[37]. The knock-on effect of habitat interventions that fail to achieve the required impact on physical niche conditions has been perfectly captured during studies of brook trout populations in Appalachian streams. Eight streams were studied for two years prior to restoration efforts and three years following restoration. Although trees were felled and added to the stream channel (approximately 15 trees per 300-m reach), there was no measurable increase in pool area. Consequently, there was also no measurable response of the resident brook trout (*Salvelinus fontinalis*) populations[38].

In complete contrast to the above scenarios, it is apparent that the creation of adult (as well as other life-cycle stage) salmonid habitat can be highly successful when applied to appropriate systems. A review of 33 projects: 17 in the USA, four in Canada, four in Japan, three in Australia, and one in each of five other countries (Ireland, England, Sweden, Liechtenstein, and Venezuela) found that structures that successfully create scour pools and cover were accompanied by marked improvements in salmonid – and other fish - populations[39]. The review process lead to the generation of some simple guidelines to help ensure the appropriateness, and attendant success, of restoration works (reproduced as Table 1.- below). The authors stress that addition of LWD structures should be viewed as either interim and/or complementary measures to improve fish populations; with the overall aim to return natural catchment scale natural processes the system[39]. The importance of *processes* as well as physical condition of habitat – specifically the input of LWD followed by the attendant scour, deposition and coarse woody debris accumulation processes – is also echoed by other authors (e.g.[40]).

Table 1: Guidance on LWD rehabilitation reproduced from[39]

Aquatic eco-systems	**Functional wood structures**	**Expected effects on fish**	**Applicable conditions or configuration of wood structure**
Moderately sized high gradient stream	Log dam Log deflector Log jam Cover	Pool and cover created by these wood structures provide winter habitat for salmonids and thus increase smolt abundance. Log jams increase species richness and abundance of tropical fish species. However, no beneficial effects on benthic fish are expected	Wood addition should be limited to streams with bed gradient of ≤3%.Wood pieces or structures should be sufficiently large compared with dominant bed materials. A combination of pool-forming and cover-creating wood structures is recommended
Moderate-ly sized low gradient stream	Half log Cover	These cover-creating wood structures provide habitat for various fish assemblages and function as refuge habitat during the dry season. In some cases, pool-forming wood structures, such as log dams, may create fish	Wood addition should be limited to physically stable streams. Physical failure easily occurs in sand-slugged or erodible streams. Wood devices that create complex instream cover are recommended

Aquatic eco-systems	Functional wood structures	Expected effects on fish	Applicable conditions or configuration of wood structure
		habitat	
Large river	Engineered log jam	Engineered log jams provide habitat for many fish species including salmonids at a local scale	Engineered log jams should be constructed to simulate natural log jams, and the use of whole trees or all parts of a tree is recommended
Side-channel habitat	Log jam	Log jams enhance winter survival for salmonids and may provide cover for many fish species	Use of large log jams with abundant root wads, branches, and bark is recommended
Lentic system (reservoir, pond, lake)	Log jam Half log Cover	These structures function as cover for fish in the long term	To enhance long-term effects on fish, the addition of wood in systems not receiving a large sediment supply is recommended. Woody cover functions at sites without substrates and macrophytes
Estuary	Log jam Cover	Epibenthic fish respond positively to the addition of wood during the summer. No other significant evidence has been obtained	Use of log jams is recommended. However, further studies are required prior to initiation of rehabilitation projects

A further meta analysis of 211 stream restoration projects examined the effect of restoration projects that used weirs, deflectors, cover structures, boulder placement, and large woody debris introduction on salmonid abundance[41]. Significant increases in the average depth and area of pool habitat along with the amount of LWD and percentage of cover habitat were all noted. The attendant biological response to these habitat changes had an average (mean) effect size of a 167% increase in salmonid density, and a 162% increase in salmonid biomass[41]. However, the 211 datasets comprised relatively short-term investigations – and greater understanding of longer-term effects was called for [41].

In order to address valid and widespread requirements for understanding longer-term effects of LWD additions, research has been performed for over two decades in Colorado streams. Adult brown trout density rapidly increased in treatment sections following LWD introductions during 1988. The LWD produced measurable increases in pool habitat volume (>3x greater than control reaches). In addition, the brown trout population density remained 53% higher in LWD-addition reaches than control reaches 21 years later[42]. The authors stress that the efficacy of increasing scour pool formation and cover provision depends on adult habitat being the limiting factor[42].

Summary Conclusions

Overall, a number of clear messages emerge from the review of existing literature on salmonid ecology and restoration of their habitats. In particular:

- The habitat requirements for brown trout, and other salmonid fish, are well defined in a wealth of literature
- The success of any restoration project critically depends on the need to identify the key impacts on a given river system
- Many of these key impacts can over-ride any influence of structural alterations e.g.
    - water quality
    - flow regime
    - riparian land-use
    - climatic interactions with each of the above
- It is imperative to identify the correct habitat bottleneck(s) to target and to provide access to high quality habitat required for the entire lifecycle.
- A sufficiently large change in the physical environment must be achieved in order to effect a response in the biota (i.e. genuinely bring conditions back within niche limits)
- Failure to observe any of the above considerations is likely to be accompanied by a failure of fish populations and other biota to respond to any habitat manipulation

These findings do indicate that, when applied correctly, habitat restoration can be a vital component of aiding the ecological recovery of watercourses. Physical in-stream habitat quality is one of the fundamental pillars of a healthy river – with other prominent (and inter-related) examples being flow-regime, sensitive management of the surrounding catchment and water quality. There is a critical requirement for correct problem diagnosis and mitigation measures that are sufficient to bring physical and chemical conditions back within niche requirements. It is important to remember that such niche requirements must account for full-lifecycle processes, rather than providing only for isolated stages of development. Consequently, there is a crucial implied role for expert input into both diagnosis and solution design. These expert roles will be found within the WTT and also through partnership with other specialist organisations such as, amongst others, the Rivers Trust, River Restoration Centre, local River Authorities (e.g. Environment Agency, Scottish Environmental Protection Agency, Northern Ireland Environment Agency and Environmental Protection Agency Ireland), The Grayling Society, Centre for Ecology and Hydrology as well as private river restoration consultancies.

References

1. Hutchinson, G.E., *Concluding remarks, Cold Spring Harbor Symposium.* Quantitative Biology, 1957. **22**: p. 415-427.
2. Armstrong, J.D., et al., *Habitat requirements of Atlantic salmon and brown trout in rivers and streams.* Fisheries Research, 2003. **62**(2): p. 143-170.
3. Al-Chokhachy, R. and B.B. Roper, *Different Approaches to Habitat Surveys Can Impact Fisheries Management and Conservation Decisions.* Fisheries, 2010. **35**(10): p. 476-488.
4. Crisp, D.T. and P.A. Carling, *Observations on Siting, Dimensions and Structure of Salmonid Redds.* Journal of Fish Biology, 1989. **34**(1): p. 119-134.
5. Essington, T.E., P.W. Sorensen, and D.G. Paron, *High rate of redd superimposition by brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) in a Minnesota stream cannot be explained by habitat availability alone.* Canadian Journal of Fisheries and Aquatic Sciences, 1998. **55**(10): p. 2310-2316.

6. Grost, R.T., W.A. Hubert, and T.A. Wesche, *Redd Site Selection by Brown Trout in Douglas Creek, Wyoming.* Journal of Freshwater Ecology, 1990. **5**(3): p. 365-371.
7. Kondolf, G.M., *Assessing salmonid spawning gravel quality.* Transactions of the American Fisheries Society, 2000. **129**(1): p. 262-281.
8. Kondolf, G.M. and M.G. Wolman, *The Sizes of Salmonid Spawning Gravels.* Water Resources Research, 1993. **29**(7): p. 2275-2285.
9. Ottaway, E.M., et al., *Observations on the Structure of Brown Trout, Salmo-Trutta Linnaeus, Redds.* Journal of Fish Biology, 1981. **19**(5): p. 593-607.
10. Raleigh, R.F., L.D. Zuckerman, and P.C. Nelson, *Habitat suitability index models and instream flow suitability curves: Brown trout. Revised.* 1986, U. S. Fish and Wildlife Service Biological Report.
11. Shirvell, C.S. and R.G. Dungey, *Microhabitats Chosen by Brown Trout for Feeding and Spawning in Rivers.* Transactions of the American Fisheries Society, 1983. **112**(3): p. 355-367.
12. Witzel, L.D. and H.R. Maccrimmon, *Redd-Site Selection by Brook Trout and Brown Trout in Southwestern Ontario Streams.* Transactions of the American Fisheries Society, 1983. **112**(6): p. 760-771.
13. Zimmer, M.P. and M. Power, *Brown trout spawning habitat selection preferences and redd characteristics in the Credit River, Ontario.* Journal of Fish Biology, 2006. **68**(5): p. 1333-1346.
14. Louhi, P., A. Maki-Petays, and J. Erkinaro, *Spawning habitat of atlantic salmon and brown trout: General criteria and intragravel factors.* River Research and Applications, 2008. **24**(3): p. 330-339.
15. Palm, D., et al., *Influence of European sculpin, Cottus gobio, on Atlantic salmon Salmo salar, recruitment and the effect of gravel size on egg predation - implications for spawning habitat restoration.* Fisheries Management and Ecology, 2009. **16**(6): p. 501-507.
16. Palm, D., et al., *The influence of spawning habitat restoration on juvenile brown trout (Salmo trutta) density.* Canadian Journal of Fisheries and Aquatic Sciences, 2007. **64**(3): p. 509-515.
17. Armstrong, J.D. and K.H. Nislow, *Critical habitat during the transition from maternal provisioning in freshwater fish, with emphasis on Atlantic salmon (Salmo salar) and brown trout (Salmo trutta).* Journal of Zoology, 2006. **269**(4): p. 403-413.
18. Elliot, J.M., *Quantitative ecology and the brown trout*. Oxford Series in Ecology and Evolution, ed. R.M. May, Harvey, P.H. 1994, Oxford: Oxford University Press.
19. Miyakoshi, Y., et al., *Importance of instream cover for young masu salmon, Oncorhynchus masou, in autumn and winter.* Fisheries Management and Ecology, 2002. **9**(4): p. 217-223.
20. Kennedy, B.P., K.H. Nislow, and C.L. Folt, *Habitat-mediated foraging limitations drive survival bottlenecks for juvenile salmon.* Ecology, 2008. **89**(9): p. 2529-2541.
21. Boss, S.M. and J.S. Richardson, *Effects of food and cover on the growth, survival, and movement of cutthroat trout (Oncorhynchus clarki) in coastal streams.* Canadian Journal of Fisheries and Aquatic Sciences, 2002. **59**(6): p. 1044-1053.
22. Millidine, K.J., J.D. Armstrong, and N.B. Metcalfe, *Presence of shelter reduces maintenance metabolism of juvenile salmon.* Functional Ecology, 2006. **20**(5): p. 839-845.
23. Harwood, A.J., et al., *Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids.* Canadian Journal of Fisheries and Aquatic Sciences, 2002. **59**(9): p. 1515-1523.
24. Hojesjo, J., J. Johnsson, and T. Bohlin, *Habitat complexity reduces the growth of aggressive and dominant brown trout (Salmo trutta) relative to subordinates.* Behavioral Ecology and Sociobiology, 2004. **56**(3): p. 286-289.
25. Koljonen, S., et al., *Body mass and growth of overwintering brown trout in relation to stream habitat complexity.* River Research and Applications, 2012. **28**(1): p. 62-70.

26. Metcalfe, N.B. and P. Monaghan, *Compensation for a bad start: grow now, pay later?* Trends in Ecology & Evolution, 2001. **16**(5): p. 254-260.
27. Solazzi, M.F., et al., *Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams.* Canadian Journal of Fisheries and Aquatic Sciences, 2000. **57**(5): p. 906-914.
28. Everall, N.C., et al., *Ecological benefits of creating messy rivers.* Area (Royal Geographical Society), 2012: p. 1-9.
29. Elliott, J.M., *Mechanisms Responsible for Population Regulation in Young Migratory Trout, Salmo-Trutta .I. the Critical Time for Survival.* Journal of Animal Ecology, 1989. **58**(3): p. 987-1001.
30. Muotka, T. and J. Syrjanen, *Changes in habitat structure, benthic invertebrate diversity, trout populations and ecosystem processes in restored forest streams: a boreal perspective.* Freshwater Biology, 2007. **52**(4): p. 724-737.
31. Wesche, T.A., C.M. Goertler, and C.B. Frye. *IMPORTANCE AND EVALUATION OF INSTREAM AND RIPARIAN COVER IN SMALLER TROUT STREAMS*. in *Riparian Ecosystems and Their Management: Reconciling Conflicting Uses First North American Conference*. 1985. Tucson, Arizona: Wyoming Water Research Center University of Wyoming Laramie, Wyoming.
32. Lehane, B.M., et al., *Experimental provision of large woody debris in streams as a trout management technique.* Aquatic Conservation-Marine and Freshwater Ecosystems, 2002. **12**(3): p. 289-311.
33. Lepori, F., et al., *Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity?* Ecological Applications, 2005. **15**(6): p. 2060-2071.
34. Palmer, M.A., H.L. Menninger, and E. Bernhardt, *River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice?* Freshwater Biology, 2010. **55**: p. 205-222.
35. Stewart, G.B., et al., *Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review.* Ecological Applications, 2009. **19**(4): p. 931-941.
36. Vehanen, T., et al., *Effects of habitat rehabilitation on brown trout (Salmo trutta) in boreal forest streams.* Freshwater Biology, 2010. **55**(10): p. 2200-2214.
37. Rosenfeld, J.S. and L. Huato, *Relationship between large woody debris characteristics and pool formation in small coastal British Columbia streams.* North American Journal of Fisheries Management, 2003. **23**(3): p. 928-938.
38. Sweka, J.A. and K.J. Hartman, *Effects of large woody debris addition on stream habitat and brook trout populations in Appalachian streams.* Hydrobiologia, 2006. **559**: p. 363-378.
39. Nagayama, S. and F. Nakamura, *Fish habitat rehabilitation using wood in the world.* Landscape and Ecological Engineering, 2010. **6**(2): p. 289-305.
40. Elosegi, A., L. Flores, and J. Diez, *The importance of local processes on river habitat characteristics: A Basque stream case study.* Limnetica, 2011. **30**(2): p. 183-196.
41. Whiteway, S.L., et al., *Do in-stream restoration structures enhance salmonid abundance? A meta-analysis.* Canadian Journal of Fisheries and Aquatic Sciences, 2010. **67**(5): p. 831-841.
42. White, S.L., et al., *Response of trout populations in five Colorado streams two decades after habitat manipulation.* Canadian Journal of Fisheries and Aquatic Sciences, 2011. **68**(12): p. 2057-2063.